A Remarkable Crustacean Parasite, and its Bearing on the Phylogeny of the Entomostraca.

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With Plate VIII.

In a decalcified specimen of Bathyactis symmetrica, dredged on the expedition of H.M.S. "Challenger" from a depth of 2300 fathoms (Lat. 35°41′ N., Long. 157°42′ E., Station 241), I was fortunate enough to meet with the remarkable parasite for which I propose the name of Petrarca bathyactidis, gen. et sp. n. Its morphological interest, and the improbability that further material will be obtained for some time, are justification sufficient for the presentation of an account which is unavoidably incomplete, owing to the minuteness of the animal and to the fact that only three specimens have been at my disposal.

Petrarca is a member of that curious family of Crustaceans, of which the Laura gerardiæ of Lacaze-Duthiers ('Mém. Ac. Sci. Inst. France,' xlii, 1883), and the Synagoga mira of Norman ('Rep. Brit. Assoc.,' 1887, p. 86), are the only other examples, a family of parasites or semi-parasites upon Anthozoa, generally regarded as forming a part of the class Cirrhipedia. To the question of the zoological position, reference will be made after a description of so much of the anatomy as it has been possible to discover.

As to its occurrence, the specimens were all found in the mesenterial chambers of a single Bathyactis; their presence had produced a certain deformation of the coral, which was recognisable from the exterior, and which probably consisted merely of an exaggerated growth of the septa at that point. In no other Bathyactis individual, either from the same or from other localities, could I find traces of further specimens of the Crustacean. Judged by the contents and appearance of the alimentary canal of Petrarca, it seems probable that its relation to its host is not a case of true parasitism, but that it sucks in the nutritive fluid produced by the digestion and maceration of the food of Bathyactis, and does not derive sustenance directly from the tissues of the polyps. It is in fact a case of commensalism in the sense defined by De Bary (' Tagebl. Vers. Deutscher Naturforsch. u. Aertzte,' 1878, p. 121) [see note, p. 119].

On an external view (figs. 1, 2) the animal is seen to be nearly spherical, measuring 1·5—1·8 mm. in diameter. The general relations of the body, limbs, and carapace are those of a Lepas without a peduncle, with the terminal penis bent forwards under the thorax, the limbs much reduced, the mantle not carrying calcareous plates, but greatly swollen by the growth of the internal organs into its substance. The carapace thus formed is a dorsal and lateral outgrowth from the anterior part of the thorax (not merely from the neck as in Lepas), leaving free the head end and the posterior part of the body. Between the two halves of the carapace are seen, in an external and ventral view (fig. 1), the head, some of the appendages, and the penis. The ventral part of the carapace is spinose, the dorsal smooth.

On removing the carapace from one side the appendages come into view (fig. 3). A pair of pre-oral appendages or antennæ extend forwards in fig. 1, both of which were visible in the specimen drawn in fig. 3 (the remaining appendages in this figure are those of the left side only). They are terminated by two strong dorsally-directed hooks, one of which, the strongest, is articulated to the limb; between these projects on the ventral side a delicate-jointed spine (fig. 6). Besides these terminal joints the limb is divided into three sections, which are flexed into the shape of a Z, the last joint being directed dorsally. Posteriorly to the antennæ is placed the oral cone (*or. c.* of fig. 3) upon which the mouth opens, and in which lie a pair of weak crushing mandibles; the latter were clearly recognisable in transverse sections, but their exact shape could not be ascertained. The oral cone is deeply grooved in the median line in a manner suggesting the fusion of two lateral plates. Behind the oral cone are placed six pairs of (thoracic) appendages (i—vi, fig. 3), of which the first are long, slender, and uniramose, the five posterior pairs being reduced to simple leaf-like flabella; they are all devoid of hairs or spines. The body is then prolonged into a trumpet-shaped penis slightly bifid at the free end, which bends forward along the ventral surface between the appendages of the two sides. From the base of this projects backwards a bilobed knob probably representing the abdomen; at this point commences the dorsal curvature, a slight segmentation being recognisable before the posterior junction of the carapace with the thorax is reached.

The epidermis, a single layer of flattened cells, is covered over the whole surface of the body, carapace, and appendages, by a thin chitinous cuticle; though a calcareous layer might have been removed by the action of the decalcifying fluid in which the Bathyactis had been placed, no histological evidence of such a deposit is forthcoming. The spines on the carapace are simply outgrowths of the cuticle and epidermis, and show no trace of a nervous or nutritive function. The perivisceral space underlying the outer body wall does not appear to be sharply bounded on the parietal surfaces. Muscles (striated), individual muscle-fibres, and connective-tissue strands run through it; at some points the parietal surfaces appear to be discontinuously lined by large roundish cells, of a markedly yellowish tint and very granular contents; it is possible that the discontinuity of this layer is due merely to the method of preservation. The splanchnic surfaces are lined by small flattened cells; no epithelial layer surrounds the muscles or generative organs. In the specimens drawn in figs. 3—5 the perivisceral space is very large, but with the maximum development of the generative organs it becomes almost entirely obliterated.

The alimentary canal (figs. 3—5) commences with a long stomodæum which bends upwards and backwards to about the centre of the body; here it meets with the hypoblastic section of the tract, into which it projects as a papilla without direct continuity of the embryonic layers. From this point runs backwards what is probably the representative of the true intestine, terminating blindly at the base of the penis (*int.*); it is also continued forwards into the head region (int^1.), and sends a third offset upwards and backwards under the dorsal wall of the carapace (int^2.); all three cæca lying in the median plane of the body. Just behind the entrance of the stomodæum into the intestine are given off at right angles the hepato-pancreatic diverticula, bending outwards and backwards into the carapace (int^3.), and branching into smaller cæcal lobes (the gland of the left side has of course been removed with that half of the carapace in fig. 3). The lining membrane of the hepatopancreas and alimentary canal consists throughout of well-marked cubical cells, showing no specialisation in any particular region.

The nervous system (coloured black in figs. 3, 5) consists of a minute supra-œsophageal mass of transverse nerve-fibres devoid of nerve-cells (a curious result of the degraded habit of life), of two circumœsophageal commissures with nerve-cells, and of a comparatively thick ventral cord well supplied with cells. The latter is apparently not differentiated into ganglia, but gives off nerves dorsally to the surrounding tissues. No branches of importance are given off to the appendages; no eyes or other sense-organs were recognisable.

The animal is hermaphrodite. The testes (figs. 4, 5) are paired, and consist of one or more lobes on each side, lying posteriorly in the carapace among the hepatic cœca. The diagrammatic figure 4 is taken from a specimen in which the generative organs had not reached their maximum development, although the vasa deferentia were charged with apparently ripe spermatozoa; in another specimen they completely filled the dotted area marked *te*^{1}., obliterating the dorsal and posterior region of the perivisceral space. Each lobe of the testis is divided into lobules, and the contents of each lobule are all at the same stage of spermatogenetic development. The whole organ, as well as each separate lobule, is surrounded by a thin, structureless, connective-tissue capsule, and no perivisceral epithelium lines the capsule externally. A testicular epithelium of cubic cells with large round nuclei is generally visible internally on the proximal side of the organ, from which presumably the groups of sperm-cells are derived; it is not visible among or around the lobules themselves. In fig. 7 are represented such stages of the spermatogenesis as occurred in the sections, arranged as far as possible in developmental order and forming an incomplete series; in the organ itself, however, the position of a lobule in the testis bears no relation to the stage of development attained by its contents, and the number of sperm-cells included appears also to be variable. In stage I a number of germinal cells are already encapsuled, which in stage II have proliferated; the cells then appear to enlarge, and the granules of the nucleus, which presumably represent the nodes of the nuclear reticulum, stain more deeply; the round nucleus is then replaced by chromatic loops (stage IV), and division appears to take place resulting in the formation of cells with small highly-chromatic nuclear loops (stage V). At this point there is a wide gap in the series which I am unfortunately unable to bridge, stage VI representing spermatozoa forming a loose reticulum of thin strands. The reticulum becomes closer, the spermatozoa thicken and stain very deeply (stage VII), and then arrange themselves with their longer axis more or less parallel (stage VIII). In the vas deferens itself they resemble the last-mentioned stage, and lie with their longer axes parallel to each other and to the tube. The vasa deferentia on each side pass directly to the end of the penis, on which they open separately.

The **ovary** (figs. 4, 5) forms a lobate mass on each side of the intestine, lying mainly in the carapace in a position anterior and ventral to that of the testis. The two halves are connected by a bridge which lies dorsal of the intestine, just behind the point where the dorsal cæcum is given off. In this region are to be found the youngest ova, which pass from here right and left into the peripheral parts of the organ as they ripen. They appear to be budded off from the follicular epithelium which lines the whole of the organ. In the condition of maximum development the ovary extends forward, obliterating the perivisceral space and filling the dotted area marked *ov*^{1}. in fig. 4. The oviduct I have not been able to identify with certainty, but a structure which may be of that nature starts from the proximal edge of the ovary near the median bridge, and runs ventrally towards the region of the first thoracic appendage. It is probably visible with certainty only during the passage of an ovum; the vasa deferentia would have been similarly unrecognisable but for their being charged with spermatozoa for nearly their whole length.

With regard to other structures in the body, a large mass of cells (*gl.* in figs. 4, 5) lies on each side of the intestine between the union of the stomodæum and that of the hepatic diverticula with the alimentary canal. This gland, as it may be called, is not surrounded by any connective-tissue capsule or perivisceral epithelium, and consists of cells with large round nuclei, and strongly suggesting germinal cells in their histological appearance. Against this possibility, however, argue the facts that they are not in contact with the ovary at any point, and that the youngest ova are to be found in the median bridge mentioned above as connecting the two halves of the ovary. No duct appeared to be connected with these "glands," and they are not continuous with each other below the intestine. A glandular mass in nearly the same position was recorded by Lacaze-Duthiers in his account of Laura.

Starting in the oral cone, apparently in a loose network of connective tissue, a duct with clearly defined lumen runs backwards to open at the base of the (first or) second appendage. As to the function or homology of this duct, I have no suggestion to offer at present.

A large digastric occlusor muscle lies on the ventral side of the stomodæum, close to its entrance into the intestine, and just in front of the gland of unknown significance mentioned above. It is omitted in the diagrams for clearness sake.

Relation of Petrarca to Laura and to Synagoga:—the Ascothoracida.

Of Synagoga, we have at present only the short preliminary account by Norman ('Rep. Brit. Assoc.,' 1887, p. 86), dealing merely with the external characters. From this it appears that it strongly resembles Laura, but that the appendages have undergone less degeneration.

Laura gerardiæ[1] ('Mem. Ac. Sci. Instit., France,' xlii, 160 pp., viii pls.) is parasitic on, and overgrown by, the polyps of Gerardia, an Antipatharian genus from the Mediterranean coast of Africa. It is adherent to the stock of its host by a remarkable development of processes on the carapace, which grow in among the tissues of Gerardia, and are probably nutritive in function. The carapace is an elongate sac within which the animal lies (l. c., pl. i, figs. 1, 2) and is thus formed: a narrow stalk-like outgrowth from the head[2] becomes almost at once an enormous fan-shaped expansion (l. c., pl. ii, fig. 15; pl. iii, fig. 25), measuring up to 4 cm. in length; and the two expansions fuse along the dorsal and ventral lines except for one small opening. The animal, generally less than 1 cm. in length, is to be found near this opening, towards which both cephalic and anal regions are directed; it is divisible into the following regions (l. c., pl. iii, fig. 25): (1) a large dome-shaped swelling, regarded by Lacaze-Duthiers as the head [but which is probably an exaggerated buccal cone]; it is grooved ventrally and anteriorly, and at the summit of the groove is placed the buccal armature, an arrangement of styliform pieces

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[1] Matter additional to Lacaze-Duthiers' original description is enclosed in square brackets.

[2] Query: on each side? Neither from the figures nor description have I been able to infer with certainty whether one median dorsal or two dorso-lateral outgrowths give origin to the carapace.

[? = mandibles + maxillæ i] of some complexity; (2) a complete ring-shaped segment [the true head] from which the antennæ take origin, and from which grow out the stalks which expand into the carapace. [The position of the antennæ, and of the supra-œsophageal ganglion (l. c., pl. iv, fig. 44) seem to leave no doubt that this part corresponds to the true head.] Ventrally this [head] bears a pair of [sucker-like] swellings, as to the nature of which the French Professor expresses himself in doubt; in one place (p. 70), stating that they may, "morphologiquement peut-être, représentent quelques paires ou pièces buccales ou appendices supérieurs;" at another (p. 148), styling them " antennules, ou tubercles sous-céphaliques." [Being post-oral and ventral they can hardly be regarded as antennules, and may possibly correspond to a (second) pair of maxillæ.] (3) The next region consists of six complete [thoracic] segments, each bearing a pair of simple uniramose limbs. At the base of the first pair open the oviducts; in the bases of the succeeding four pairs lie the testes, opening on the basal joint by a number of small tubules; the last, or sixth pair, has no connection with the generative organs. (4) Behind this [thoracic] region come three limbless [abdominal] segments, with the last of which articulate a pair of stout caudal spines. In the carapace lie a strong adductor muscle, and the hepato-pancreatic and ovarial cæca, the latter opening as mentioned above at the base of the first [thoracic] limb, and connected with each other by a bridge above the intestine [as in Petrarca]. The œsophagus [stomodæum] projects on a papilla into the intestine (l. c., pl. iv, fig. 44); the latter, after giving off a hepato-pancreatic cæcum into the carapace on each side, passes to the caudal region, where Lacaze-Duthiers was unable to demonstrate the presence of an anus. [The nervous system consists of the same parts as that of Petrarca described above.] A Nauplius, and probably also a Cypris-larva (cf. l. c., p. 137, pl. viii, fig. 102), occur in the development.

On comparing Petrarca with this description, it is at once apparent that the new type has undergone a much greater degradation. No head region is distinctly marked off as such, only one pair of mouth appendages is recognisable, the thoracic appendages are reduced to a far simpler character, the abdominal region has almost disappeared, and segmentation occurs only in the posterior region of the body.

On the other hand, the resemblances that exist between the two forms are so marked that it is impossible to doubt of a close genetic relationship. The similar habit of parasitism upon Anthozoa, the presence of a large lateral carapace into which penetrate the organs of digestion and of reproduction, the similar construction and dorsal flexure of the antennæ, the presence of six pairs of thoracic appendages and of a more or less reduced abdomen, the hermaphroditism (a rare feature among Crustacea), are ordinal characteristics of these two animals and of Synagoga, and are found in no other single group. We may unite them under the name **Ascothoracida**, suggested by Lacaze-Duthiers, and accepted by Norman in his account of Synagoga.

The main differences between Laura and Petrarca, in addition to those mentioned above as being indicative of a further degradation, are: (1) the extension of the carapace over a larger number of segments in Petrarca; (2) the development by the latter of two additional median cæca on the intestine; and (3) the position of the testes. With regard to this latter point, it is interesting to note that while in Petrarca the testes are in the thorax, and in Laura at the bases of certain of the limbs, they occur in (adult) Cirrhipeds in both regions, lying above the nerve-cord and filling the protopodite of the first five and sometimes also of the sixth pairs of legs.

RELATION OF THE ASCOTHORACIDA TO THE CIRRHIPEDIA AND OSTRACODA.

It was stated above that the characteristics of the Ascothoracida are found in no other single group, but they are so markedly shared between the Cirrhipedia and Ostracoda as to suggest that they may indicate a genetic relationship between these two groups. Though it is customary to assume that degeneracy is a necessary consequence of parasitism, few more favorable conditions for the preservation of ancestral characteristics could be found than those of an animal which adopted, at an early period of biological time, a semi-parasitic (commensal) habit upon hosts exposed to no special dangers,[1] and would therefore not be subjected to any violent struggle for existence, provided always that some means for reaching its host be retained for at least the duration of larval life. Such conditions are realised by the Ascothoracida: a free larval existence (judging from the development of Laura) brings them either to an Antipatharian or a Bathyactis, both well protected by skeleton and nematocysts, and in the latter instance at a depth where the struggle does not seem to be severe.

The agreement of the Ascothoracida with the Lepadidæ (the least modified of Cirrhipedia) is very strongly marked. While it is impossible to present a definition of the latter group which shall include all its characteristics, it will yet be admitted that the presence of only one pair of antennæ in the adult, of an indifferently-segmented thorax bearing six pairs of appendages (biramose in Synagoga), of a rudimentary abdomen, on the ventral side of which springs an enormous penis, of an oviducal opening at the base of the first thoracic limb (Hoek, Cirrhipedia [anatomical part], 'Chall. Rep. Zool.,' vol. x), and the position of the testes in the bases of the thoracic appendages, are all features of prime morphological importance, which characterise the Lepadidæ and are shared among the Ascothoracida. The presence of shell-pieces on the mantle of the one, and the reduction of the mouth parts and simplification of the appendages in the other, are characters of secondary value, dependent on their different modes of life.

While the points of resemblance to the Cirrhipedia are so strong and so numerous, the presence of a bivalve carapace, which is not a mere lamina composed mainly of epidermic structures, but a capacious lateral outgrowth of the body itself into which the organs of reproduction and digestion are continued, is a feature confined among Crustacea to the Ascothoracida and the Ostracoda; a limitation the more remarkable, since in almost every group, both of Entomostraca and Malacostraca, occur examples of the development of a protective carapace.

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[1] If the host be modified in accordance with changing or unfavorable conditions, modifications will probably be also induced in the parasite.

Allowing to these facts the weight which I would assign to them, the Cirrhipedia and Ostracoda are brought into more intimate relations than has hitherto been admitted.

Since the phylogenetic significance of the Nauplius larva, and more especially the value of its subsidiary features, is still under discussion, it is enough to say here that there is no such violent discrepancy between the early Nauplius of Balanus (the most typical among Cirrhipeds) and that of Laura, the only Ascothoracidan with whose development we are acquainted, as to necessitate a separation between these two groups. The Nauplius of Ostracoda presents a very different appearance from the two just mentioned; it is, when freed, already enclosed in a bivalve shell, and presents the lateral flattening characteristic of the adult; on the other hand, the so-called Cypris-stage in the development of Cirrhipedia brings the two groups into close proximity. As to its phylogenetic value, "it is clear that the Cypris-stage represented more or less closely an ancestral form of the Cirrhipedia, and that both the large bivalve shell and the large compound eyes were ancestral characters. These characters would seem incompatible with Copepod affinities, but point to the independent derivation of the Cirrhipedia from some early bivalve Phyllopod form" (Balfour, 'Comp. Embryol.,' i, p. 424). The mention made by Balfour of Copepoda refers to the views of Claus on the matter, which are most simply expressed by reproducing his table of the descent of the Entomostraca[1] (the Protostraca are the "Urphyllopoden" of his earlier writings):

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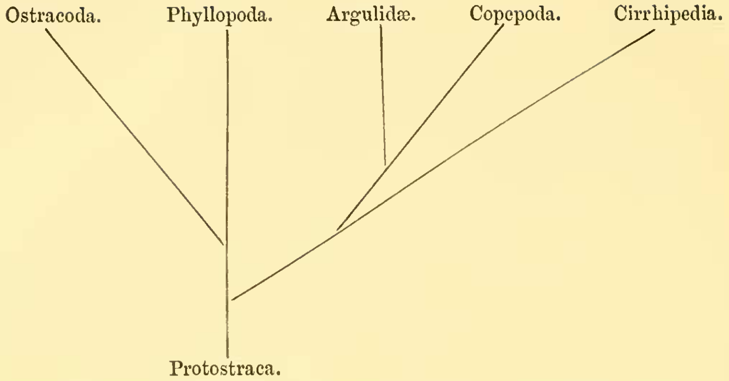
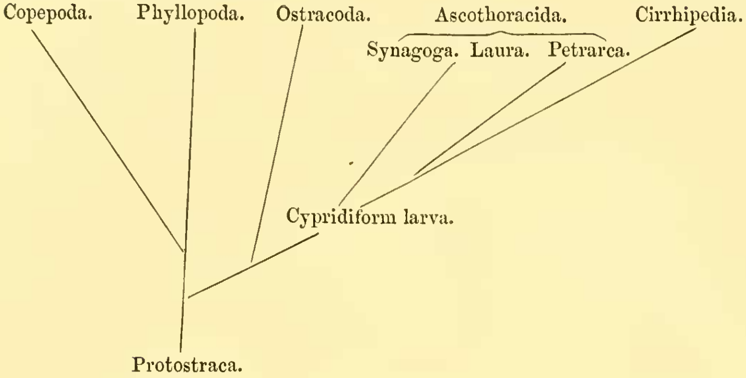
[1] This phylogeny is indicated in the "Untersuchungen zur Erforschung der genealogischen Grundlage des Crustaceen-systems" (Wien, 1876, 4to), and the table taken from the "Neue Beiträge zur Morphologie der Crustaceen," 'Arb. Zool. Inst. Wien,' vi, p. 105.



With regard to the supposed close relationship between Cirrhipedia and Copepoda, so clearly indicated by Claus in this table, I again quote from Balfour a passage which, I believe, expresses the views of most zoologists on the matter: "The Cirrhipedia are believed by Claus to belong to the same phylum as the Copepoda. This view does not appear to be completely borne out by their larval history. The Nauplius differs very markedly from that of the Copepoda, and this is still more true of the Cypris stage. The Copepod-like appendages of this stage are chiefly relied upon to support the above view, but that form of appendage was probably very primitive and general, and the number . . . does not correspond to that in Copepoda. On the other hand, the paired eyes and the bivalve shell form great difficulties in the way of Claus's view" (' Comp. Embryol.,' i, p. 423). The appendages on which Claus relies consist of protopodite, exopodite, and endopodite, and are of the primitive and widely-spread type on which Milne-Edwards and Huxley first laid insistance, and which Ray Lankester has shown to have been derived at an early period of biological time from the yet more primitive Protophyllopodan (Protostracan) limb.

While both Claus and Balfour regard the Ostracoda as having originated independently of other phyla from the Protostracan stem, I would submit that the remarkable organisation of the Ascothoracida and the existence of the otherwise inexplicable Cypris-larva point rather to a descent which may be thus expressed :



The point of divergence between the phyla of the Ostracoda and Cirrhipedia would be characterised by a bivalvate organism with six pairs of thoracic appendages and some abdominal (Laura) segments, the reduction of which has proceeded further in the case of the Ostracoda than in the other groups (cf. Balfour, 'Comp. Embryol.,' i, p. 425). The existing Cypridiform larva would approximately represent the (? hermaphrodite) ancestor of Cirrhipedia and of the Ascothoracidan type, while Petrarca may be regarded as having branched off from the main stem at a later period than its two congeners, when the development of a terminal penis had been already acquired as a secondary character.

To Canon A. M. Norman and to Professor E. Ray Lankester I desire to express my obligation for valuable suggestions.

Note.—The relation of Petrarca to its host is a case which may be termed either commensalism or parasitism. On the one hand, Tænia, an undoubted "parasite," does not derive sustenance directly from its host; on the other, many Amphipoda, exhibiting no trace of degeneration, live in Anthozoa, and are generally ranked as commensals.

EXPLANATION OF PLATE VIII,

Illustrating Dr. G. Herbert Fowler's paper on "A Remarkable Crustacean Parasite."

The animal is represented in all the figures in the Cirrhipedian position, *i. e.* with the dorsal surface downwards.

abd. Abdomen.
ant. Antenna.
gl. Gland of unknown function.
int. Intestine.
int^{1}. Cephalic (median) cæcum.
int^{2}. Dorsal (median) cæcum.
int^{3}. Hepato-pancreatic (paired) cæcum.
i—vi (Fig. 3). The six thoracic appendages.
or. c. Oral cone.
ov. Ovary.
ov^{1}. Space filled by ovary in maximum development.
pe. Penis.
st. Stomodæum.
te. Testis.
te^{1}. Space filled by testis in maximum development.
v. d. Vas deferens.

Fig. 1.—The animal from the ventral surface, lying in the bivalve carapace. From the cephalic region project (downwards in the figure) the two antennæ, behind which lies the grooved oral cone. Two thin filaments behind this represent the first pair of thoracic appendages; between the next four pairs of appendages, which are flabelliform, projects forwards the terminally bilobed penis, at the base of which are seen two small lobes representing the reduced abdomen.

Fig. 2.—Dorsal view of the carapace, which completely conceals the body of the animal.

Fig. 3.—The animal from the left side, to show the alimentary system, nervous system, and appendages; the left half of the carapace, with its contents (the ovary, testis, and hepato-pancreatic diverticulum), having been removed. While both right and left antennæ were visible in this specimen, the remaining appendages are those of the left side only. The nervous system is represented in black.

Fig. 4.—Viewed from the left side, to show the reproductive organs. The appendages, the carapace, and hepatic diverticulum of the left side are removed, leaving the ovary and testis visible.

Fig. 5.—The animal is supposed to have been transversely divided, and the two halves opened. The anterior half is that on the right of the figure.

Fig. 6.—The antenna.

Fig. 7.—Diagram of the testis, showing various stages in the spermatogenesis.